

## Herd Size in Large Herbivores: Encoded in the Individual or Emergent?

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**Abstract.** In large mammalian herbivores, the increase of group size with habitat openness was first assumed to be an adaptive response, encoded in the individual. However, it could, alternatively, be an emergent property: if groups were nonpermanent units, often fusing and splitting up, then any increase of the distance at which animals perceive one another could increase the rate of group fusion and thus mean group size. Dynamical models and empirical data support this second hypothesis. This is not to say that adaptive modifications of mean herd size cannot occur. However, this changes the way in which we can envisage the history of gregariousness in large herbivores during the Tertiary.

### Introduction

Large mammalian herbivores, such as ruminants or kangaroos, make up groups that are easily recognizable in the field: they consist of individuals located a short distance from one another and most often engaged in a common activity, for example, feeding, traveling, or resting. The size of these groups is very variable and has been a matter of study for ethologists and ecologists for about 40 years.

Two general trends were early identified. First, within a species, group size tends to increase with population density

(Spinage, 1969; Johnson, 1983; Wirtz and Lörscher, 1983; Table 1). Second, herd size increases with habitat openness: whereas groups are small in forested habitats, they are much larger in grassland and other open landscapes. This second trend was initially reported in African antelope taken as a whole, considering the typical habitat and herd size of each species (Estes, 1974; Jarman, 1974). It was then recorded within species using habitats of varying openness (Leuthold, 1970; Evans, 1979; LaGory, 1986; Hillman, 1987; Table 2; Fig. 1).

These two general trends were rapidly explained in two diverging ways. As early as 1964, Caughley hypothesized that groups of large herbivores were nonpermanent units that often fused and split up. On this basis, the author suggested that any increase in population density should increase the rate of group meeting, and thus the average group size. This purely mechanistic proposal is equivalent to saying that group size is an emergent property, resulting from multiple fusion and fragmentation events, and that it is sensitive to variations of population density.

In contrast to Caughley's proposal, the variation of group size with habitat openness was assumed to be a biological adaptation, encoded in the individual. A central argument, developed by Estes (1974) and Jarman (1974), was that in closed habitat, a herbivore can easily reduce the probability of being detected by predators by being discreet and, especially, by living in small groups. By contrast, in open habitat, it is more difficult to escape notice. Being surrounded by many conspecifics should then ensure the best protection against predators because, in the event of an attack, there is a high probability that the victim will be another group member ("selfish avoidance of predators by aggregation"; Hamilton, 1971). As a consequence, natural

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Table 1

Variation of group size with population density in different species of large herbivores (*Macropus* spp. are kangaroos, which are marsupials; the other species are ruminants—i.e., eutherians)

	Study period	Habitat	Pop. density (ind./100 ha)	Group size				Reference
				Mean	SD	Range	n	
Walleroo	Year	Pasture and woodland (2)	8	1.8	1.2	1–7	233	Taylor (1982, 1983)
<i>Macropus robustus</i>			55	2.2	1.7	1–>12	1610	
Grey kangaroo	Year	Open woodland (2)	10	3.1	1.6	1–9	86	Southwell (1984a)
<i>Macropus giganteus</i>			37	4.2	2.8	1–13	220	
			91	8.5	8.3	1–65	348	
Sika deer	January	Forest (1)	60	5.5	3.9	1–?	85	Borkowski (2000)
<i>Cervus nippon</i>			120	6.8	4.3	1–?	158	
Fallow deer	Winter	Forest (1)	25	4.4	3.0	1–16	297	Vincent (unpubl. data)
<i>Dama dama</i>			31	4.6	3.1	1–20	432	
			73	5.7	4.4	1–37	473	
Dorcas gazelle	Summer	Desert (2)	0.3	2.2	1.2	1–5	9	Lawes and Nanni (1993)
<i>Gazella dorcas</i>			2	3.2	2.0	1–5	18	
Pyrenean chamois	Year	Pasture and cliff (2)	5	5.0	8.4	1–77	301	Richard-Hansen <i>et al.</i>
<i>Rupicapra pyrenaica</i>			30	7.6	10.3	1–139	1886	(1992 and unpubl. data)
Alpine ibex	Year	Pasture and cliff (1)	1	1.8	0.7	1–?	9	Toigo <i>et al.</i> (1996)
<i>Capra ibex</i>			3	2.8	2.0	1–?	117	
			7	4.5	3.7	1–?	49	

(1) A single study area supporting different population densities year to year.

(2) Different study areas supporting similar habitats but different population densities.

selection should have retained individuals preferring to be within small groups when in closed habitat, and within large groups when in open landscape.

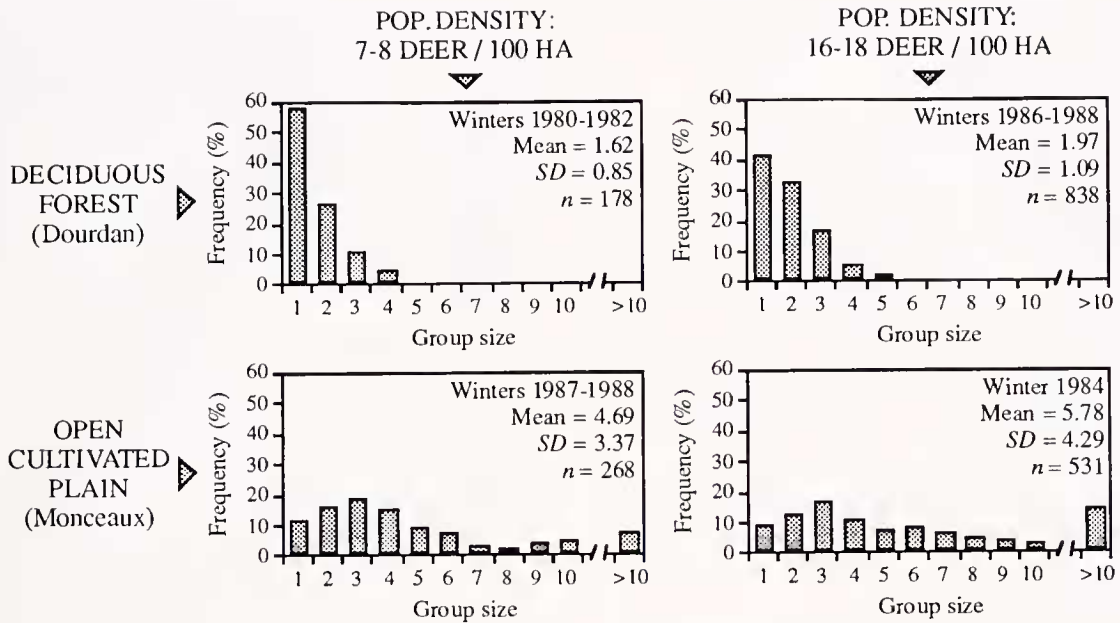
Because they relate to the effect of two different ecological factors, these contrasting hypotheses seem to have been implicitly considered as compatible, and the opposition

Table 2

Variation of group size with habitat openness in different species of large herbivores (*Macropus giganteus* is a kangaroo, which is a marsupial; the other species are ruminants—i.e., eutherians)

	Study period	Habitat	Pop. density (ind./100 ha)	Group size				Reference
				Mean	SD	Range	n	
Grey kangaroo	Winter	Closed shrubland	13	1.8	1.1	1–5	71	Southwell (1984a)
<i>Macropus giganteus</i>		Open woodland	12	3.5	1.7	1–9	24	
Moose	August	Forest	1.4*	1.6	?	1–6	146	Peek <i>et al.</i> (1974)
<i>Alces alces</i>		Alpine tundra		2.6	?	1–12	178	
White-tailed deer	Year	Forest	50*	1.9	?	1–?	197	Hirth (1977)
<i>Odocoileus virginianus</i>		Intermediate		2.5	?	1–?	872	
		Grassland		4.3	?	1–51	1667	
Axis deer	Year	Forest	5*	3.8	3.0	1–23	362	Barrette (1991 and pers. comm.)
<i>Axis axis</i>		Edge		8.3	8.2	1–100	555	
		Grassland		12.1	14.2	1–160	1889	
Fallow deer	Winter	Forest	6*	4.7	3.5	1–27	317	Schaal (1982)
<i>Dama dama</i>		Harvested maize field		15.8	12.7	1–55	349	
Grant's gazelle	Year	Bush	?	6.5	?	1–37	393	Walther (1972)
<i>Gazella granti</i>		Intermediate	?	12.5	?	1–120	125	
		Open plain	?	37.7	?	1–428	221	
Mouflon sheep	Year	Forest	?	2.1	?	1–14	?	MaiseIs (1993)
<i>Ovis gmelini</i>		Moor and woodland	?	4.4	4.1	1–61	1178	Maublanc (unpubl. data)

\* Population density estimated for the whole set of habitats.



**Figure 1.** Relative frequencies of roe deer (*Capreolus capreolus*) group sizes recorded in winter in two study areas, and for two levels of population density supported by the two areas some years apart ( $n$ : number of groups sighted, solitary animals included; after Gerard *et al.* 1995, with permission of the *Revue d'Ecologie Terre et Vie*). Group size increases with both population density (Mann-Whitney  $U$  test: in forest,  $P < 0.0001$ ; in open plain,  $P = 0.001$ ) and habitat openness (at low density,  $P < 0.0001$ ; at high density,  $P < 0.0001$ ).

between emergence and individual encoding long passed unnoticed. Moreover, the plausibility of the two hypotheses remained unquestioned for a long time. The situation has changed owing to theoretical and empirical works carried out during the 1980s and 1990s.

### Models Assuming Optimum-Size-Seeking

An important step was made when Sibly (1983) had the idea to develop and examine the properties of a dynamical model of group formation formalizing the idea that individuals exhibited preferences for group sizes shaped by natural selection.

The basic assumptions of this model are the following. First, there is a relationship between fitness and group size such that fitness is maximized for a given size (according to the rationale of Estes and Jarman, the optimal size should be small in closed habitat and large in open habitat). Second, the individuals behave as if they know which group size, in the actual environment, will give them better fitness than another: in the course of encounters, each individual leaves a group for another as soon as the size of the latter will enhance its fitness.

Although these assumptions seem to prescribe the group size that should be obtained, Sibly's model exhibits emergent properties that are rather puzzling.

1. Mean group size at equilibrium is, unexpectedly, generally larger than the optimum size. The reason for this is

not very difficult to understand. Suppose that a solitary animal encounters a group of optimal size  $s^*$ . None of the group members will leave, but the solitary individual will join the group, provided being within a group of size  $s^* + 1$  entails a better fitness than being alone. Groups still greater can form in the same way, provided their members keep a fitness higher than that of a solitary individual.

2. At equilibrium, no group shows a size lower than the optimum size, and the standard deviation of group sizes is always extremely limited ( $\leq 0.5$ ). This is inconsistent with the group size distributions actually observed in large herbivores, where small groups are rarely lacking, even when average herd size is large, and the standard deviation of group sizes can be very great, especially when the mean is large (Table 1, Table 2, and Fig. 1).

3. Mean group size at equilibrium depends on the initial group size distribution. However, it does not depend on population density. The absence of effect of population density contrasts with the effect recorded in the populations of large herbivores.

4. Groups no longer fuse or split up once the equilibrium is reached: they become permanent units. This is inconsistent with the high lability of groups revealed in an increasing number of large herbivore species since the beginning of the 1980s (Murray, 1981; Schaal, 1982; Southwell, 1984b; Fichter, 1987; Hillman, 1987; Putman, 1988; Barrette, 1991; Estes, 1991; Le Pendu *et al.*, 1995, 2000). Further-

more, this shows that Sibly's model is incompatible with the hypothesis proposed by Caughley for the increase of group size with population density.

Sibly's model was further developed during the 1980s and 1990s, by introducing altruism towards relatives and/or the possibility for group members to limit the increase of the size of their group by repelling joiners (see Giraldeau and Caraco, 2000, for a review). Indeed, the initial model ignored kin selection. Moreover, by joining a group whose size is larger than or equal to the optimal size, an individual enhanced its fitness but lowered the fitness of the group members, so that the latter could be assumed to repel the joiner. Some of these modifications of the initial model improve the first property described above in that they lead, at equilibrium, to a mean group size that tends to be closer to the optimal size. However, they do not improve the other properties of the model. So, they remain both inconsistent with the data recorded in large herbivores and incompatible with Caughley's hypothesis.

### Fusion-Fission Models

According to Caughley (1964), an increase in population density should increase the mean size of groups that frequently fuse and split up, by enhancing the rate of group encounter and thus fusion. Following the same rationale, it could be hypothesized that any increase of habitat openness, and thus of the distance at which groups can perceive one another, should increase the rate of group fusion, and thus mean group size (Gerard *et al.*, 1993). This should at least be the case, provided group fusion results from an attraction between groups. Clearly, if group fusion results from simple "collisions," then the distance at which animals can perceive one another should be without influence.

The plausibility of this hypothesis was confirmed in the mid-1990s, when Bonabeau and Dagorn (1995), Gueron and Levin (1995), and two of the authors of the present paper (Gerard and Loisel, 1995) developed new dynamical models of group formation. These models contrasted with Sibly's model in that groups were assumed to fuse and split up without any group size being preferred by the individuals. They were in fact generalizations of a previous model by Cohen (1971), in which "casual groups" were assumed to increase or decrease by a single individual (see also Okubo, 1986; pp. 45–49).

The model by Bonabeau and Dagorn (1995) is probably the simplest. First, the groups (solitary individuals included) that compose the population are assumed to move at random. Second, two groups arriving within the same portion of space systematically merge, then behave as a single group. Third, at each time step, a fraction  $p$  of the individuals leave the groups they are in by temporarily becoming solitary.

In its basic version, the model by Gueron and Levin (1995) differs from the latter in two aspects. First, two

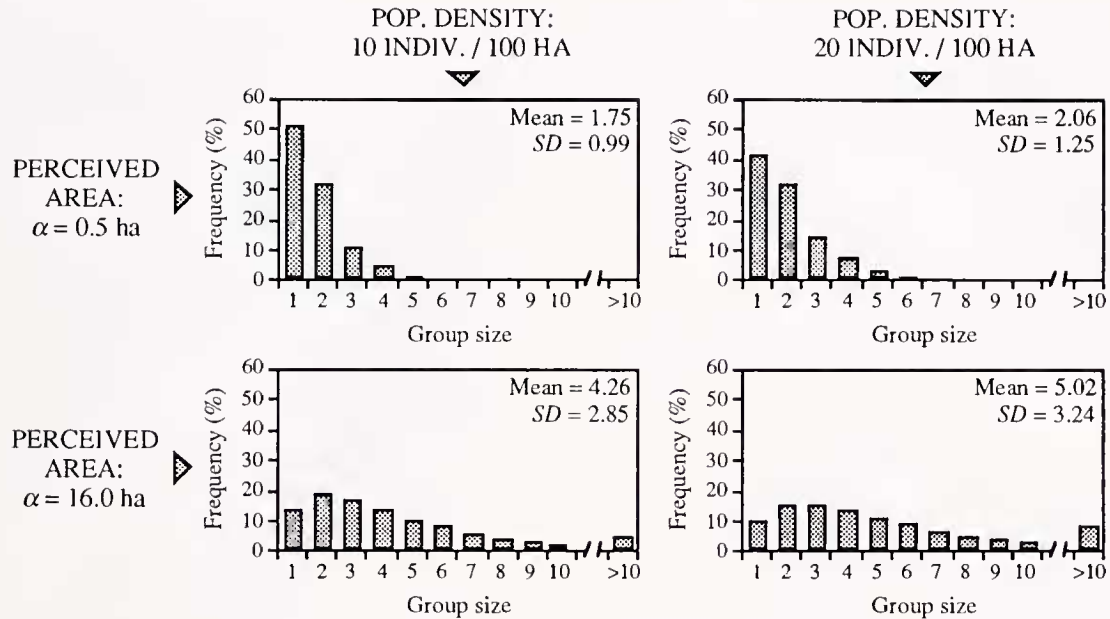
groups arriving in view of each other merge with a probability that is independent of their sizes, but not necessarily equal to 1. Second, the groups are assumed to split into two (and not only to lose single individuals) with a probability  $\beta s$ , where  $\beta$  is a constant and  $s$ , the group size. Here,  $\beta$  can be interpreted as the probability with which any individual adopts a trajectory differing from that of the other group members and is possibly followed by some of them. In practice, the size distribution of splitting groups is assumed to be uniform.

The assumptions of our model (Gerard and Loisel, 1995) are more complicated than those considered by Bonabeau and Dagorn, and Gueron and Levin. First, as is more or less implicit in the two latter models, each individual is assumed to be able to detect any conspecific present inside an area  $\alpha$ , characterizing habitat openness. Second, each individual oscillates in a probabilistic way between a "social" state and an "individualistic" state. When in the social state, an animal joins every perceived conspecific, then behaves in such a way as to stay with it. By contrast, when in the individualistic state, an animal moves without taking conspecifics into account. As a consequence, groups fuse through attraction and split up. When two individuals (or groups of individuals) in the social state perceive one another, the individuals merge and form a single group. When an individual (or a group of individuals) in the social state perceives an animal in the individualistic state, it joins it. In this case, the resulting group actually includes a leader, which is the animal in the individualistic state. However, if, within a group of this kind, a second individual turns out to be individualistic, then the group includes two leaders moving independently of each other; as a consequence, the other group members distribute themselves at random (with probability  $1/2$ ) near the two leaders, and the group splits up. The probability  $\varepsilon$  of shifting from the social state to the individualistic state and the probability  $\mu$  of the reverse shifting are fixed, so that the individual's behavior is independent of habitat openness, population density, and group size.

Though they rely on different assumptions, the Bonabeau and Dagorn model (1995), the Gueron and Levin model (1995), and our model exhibit remarkably similar emergent properties.

1. The first property that the three models have in common is that the group size distributions obtained at equilibrium resemble those ordinarily recorded in large herbivore populations: the group frequency exhibits a single maximum for isolated individuals or a small group size, then monotonously decreases with group size; moreover, the standard deviation of group sizes tends to be large when the mean is large.

2. Whatever the model, the group size distribution obtained at equilibrium for any given values of the parameters



**Figure 2.** Relative frequencies of group sizes obtained at equilibrium with the model of Gerard and Loisel (1995), for two values of population density and two values of the area perceived by the individual (after Gerard *et al.*, 1997, with permission of Hermes editions). In every case, the probabilities of individual state shifting are  $\mu = 0.9$  and  $\varepsilon = 0.1$ .

is independent of the initial group size distribution, provided population density is left unchanged.

3. Whatever the model and the values of its parameters, any increase of population density entails, at equilibrium, not only an increase of mean group size, as suggested by Caughley, but also an increase of group density (*i.e.*, the number of groups per unit area).

4. Whatever the model and the values of its other parameters, any increase of the distance at which groups can perceive one another increases mean group size at equilibrium (see Fig. 2 for an illustration with our model). Actually, in the three models, multiplying the area perceived by the individuals by a factor  $k$  has exactly the same effect on mean group size as multiplying the population density by the same factor (Gerard and Loisel, 1995; Gueron and Levin, 1995; Appendix).

### Checking Assumptions and Predictions

The fusion-fission models just described thus exhibited realistic, emergent properties. In addition, they showed that the same mechanism could be both at the origin of the increase of group size with population density and of the increase of group size with habitat openness. What remained to be checked were the main basic assumptions of the models, as well as predictions that could be deduced from their emergent properties. This is what we have begun to do in a population of roe deer (*Capreolus capreolus*) living in an open cultivated plain in Northern France (Mar-

chal, 1998; Marchal *et al.*, 1998). The data were recorded between November and April, observability being maximum at this season owing to the high proportion of plowed fields and the low height of crops in the cultivated fields (mainly winter cereal and rapeseed).

First, we checked that roe deer groups, like those of many other herbivores, were nonpermanent units. To that aim, we monitored 73 groups during 3 h or more. The proportion of these groups that had not broken up or fused with another group since the beginning of their observation decreased rapidly and regularly through time: after 2 h 38 min of observation, half had their composition altered by at least one fusion or fission event (Marchal *et al.*, 1998).

We then checked that group fusion generally involved inter-attraction, and thus perception at distance. Among the 103 fusion events observed, 3% were simple "collisions": they occurred when two groups met at a wood's corner, without having previously perceived each other (as shown by the absence of any behavior directed towards the members of the other group before the encounter, and the reactions exhibited on the encounter). In some other cases (21%), fusion followed a human disturbance. However, in 76% of the instances, fusion did result from an attraction between groups whose members indisputably perceived one another: the deer of at least one of two groups looked at the members of the other group and approached them over a distance often exceeding 100 m (Marchal *et al.*, 1998).

We also examined the causes of splitting up. Among the

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## Appendix

### Mean group size at equilibrium in the model by Bonabeau and Dagorn

We here correct an error made by Bonabeau and Dagorn (1995) when deriving the mean group size from their fusion-fission model. We further show that once the correction is made, increasing the population density or the area perceived by the individuals by a multiplicative factor  $k$  has exactly the same effect on mean group size.

#### Analytical expression of mean group size

In the model by Bonabeau and Dagorn, space is divided into  $N$  sites, the whole population included  $n$  individuals ( $n \ll N$ ), and the individuals simultaneously present within any given site are considered as the members of a single group. At each discrete time step, a fraction  $p$  of the  $n$  individuals of the population leave the group they are in as solitary animals, and are reinjected at random into the  $N$  sites. In addition, each group moves towards a randomly selected site, and the groups (and solitary individuals) entering the same site aggregate to form a single group.

As a consequence of these assumptions, the expected number of groups (i.e., the number of sites occupied)  $N^+$  varies between two successive time steps according to:

$$N^+(t+1) \approx N^+(t) + pn - \frac{[N^+(t) + pn][N^+(t) + pn - 1]}{2} \frac{1}{N}$$

The denominator of the right part of the equation is  $N$ , and not  $N^2$  as written by Bonabeau and Dagorn (1995). At equilibrium,  $N^+(t+1) = N^+(t)$ , so that the expected number of groups is approximately

$$N^+(t) = N_{\text{eq}}^+ \approx \sqrt{2Npn},$$

and the mean size of groups

$$\langle s \rangle = \frac{n}{N_{\text{eq}}^+} \approx \sqrt{\frac{n}{2pN}}$$

Mean group size therefore varies with  $\sqrt{n/N}$ , and not with  $\sqrt{n}/N$  as found by Bonabeau and Dagorn. Furthermore, once corrected, the analytical expressions of the number and mean size of groups at equilibrium become strictly equivalent to those obtained by Gueron and Levin (1995) with their own model.

#### Effect of population density and habitat openness

In the model of Bonabeau and Dagorn, groups entering the same site aggregate into a single group. So, a site can be considered as an area in which any individual perceives its conspecifics. If  $A$  designates the area available to the whole population, then the area of each site is  $\alpha = A/N$ . It follows that the mean size of groups at equilibrium is

$$\langle s \rangle = \sqrt{\frac{\alpha d}{2p}}$$

where  $d = n/A$  is the population density. It then appears that multiplying the area perceived by the individuals ( $\alpha$ ) or the population density ( $d$ ) by a factor  $k$  has exactly the same effect on the mean size of groups at equilibrium. The same is true with the model by Gueron and Levin (1995) and ours (Gerard and Loisel, 1995: appendix B).

# Self-Organization and Natural Selection in the Evolution of Complex Despotic Societies

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**Abstract.** Differences between related species are usually explained as separate adaptations produced by individual selection. I discuss in this paper how related species, which differ in many respects, may evolve by a combination of individual selection, self-organization, and group-selection, requiring an evolutionary adaptation of only a single trait. In line with the supposed evolution of despotic species of macaques, we take as a starting point an ancestral species that is egalitarian and mildly aggressive. We suppose it to live in an environment with abundant food and we put the case that, if food becomes scarce and more clumped, natural selection at the level of the individual will favor individuals with a more intense aggression (implying, for instance, biting and fierce fighting).

Using an individual-centered model, called DomWorld, I show what happens when the intensity of aggression increases. In DomWorld, group life is represented by artificial individuals that live in a homogeneous world. Individuals are extremely simple: all they do is flock together and, upon meeting one another, they may perform dominance interactions in which the effects of winning and losing are self-reinforcing. When the intensity of aggression in the model is increased, a complex feedback between the hierarchy and spatial structure results; *via* self-organization, this feedback causes the egalitarian society to change into a despotic one. The many differences between the two types of artificial society closely correspond to those between despotic and egalitarian macaques in the real world. Given that, in the model, the organization changes as a

side effect of the change of one single trait proper to an egalitarian society, in the real world a despotic society may also have arisen as a side effect of the mutation of a single trait of an egalitarian species.

If groups with different intensities of aggression evolve in this way, they will also have different gradients of hierarchy. When food is scarce, groups with the steepest hierarchy may have the best chance to survive, because at least a small number of individuals in such a group may succeed in producing offspring, whereas in egalitarian societies every individual is at risk of being insufficiently fed to reproduce. Therefore, intrademic group selection (selection within an interbreeding group) may have contributed to the evolution of despotic societies.

## Introduction

The assumption that evolution occurs through a single evolutionary process is no longer tenable (*e.g.*, see Plotkin and Odling-Smee, 1981), and multiple-level selection theories have slowly become more accepted (*e.g.*, Hogeweg, 1994; Maynard Smith and Szathmary, 1995; Mitteldorf and Wilson, 2000). Multiple-level selection processes may include some, or all, of the following factors: the multi-level character of biological systems and natural selection operating on them (Lewontin, 1970; Hogeweg, 1994; Sober and Wilson, 1998), self-organization and its consequences for evolution (Boerlijst and Hogeweg, 1991), and nonlinear genotype-phenotype mappings (Kauffman, 1993; Huynen and Hogeweg, 1994; Kauffman, 1995).

Within this framework of multiple-level selection theories, I present in this paper an example of the way in which a certain type of society may evolve. In studies of animal behavior, a distinction is usually made between two types of societies—egalitarian and despotic. In her studies of birds, Vehrencamp (1983) distinguishes between these two on the

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## Appendix

### Mean group size at equilibrium in the model by Bonabeau and Dagorn

We here correct an error made by Bonabeau and Dagorn (1995) when deriving the mean group size from their fusion-fission model. We further show that once the correction is made, increasing the population density or the area perceived by the individuals by a multiplicative factor  $k$  has exactly the same effect on mean group size.

#### Analytical expression of mean group size

In the model by Bonabeau and Dagorn, space is divided into  $N$  sites, the whole population included  $n$  individuals ( $n \ll N$ ), and the individuals simultaneously present within any given site are considered as the members of a single group. At each discrete time step, a fraction  $p$  of the  $n$  individuals of the population leave the group they are in as solitary animals, and are reinjected at random into the  $N$  sites. In addition, each group moves towards a randomly selected site, and the groups (and solitary individuals) entering the same site aggregate to form a single group.

As a consequence of these assumptions, the expected number of groups (*i.e.*, the number of sites occupied)  $N^+$  varies between two successive time steps according to:

$$N^+(t+1) \approx N^+(t) + pn - \frac{[N^+(t) + pn][N^+(t) + pn - 1]}{2} \frac{1}{N}$$

The denominator of the right part of the equation is  $N$ , and not  $N^2$  as written by Bonabeau and Dagorn (1995). At equilibrium,  $N^+(t+1) = N^+(t)$ , so that the expected number of groups is approximately

$$N^+(t) = N_{\text{eq}}^+ \approx \sqrt{2Npn},$$

and the mean size of groups

$$\langle s \rangle = \frac{n}{N_{\text{eq}}^+} \approx \sqrt{\frac{n}{2pN}}.$$

Mean group size therefore varies with  $\sqrt{n/N}$ , and not with  $\sqrt{n}/N$  as found by Bonabeau and Dagorn. Furthermore, once corrected, the analytical expressions of the number and mean size of groups at equilibrium become strictly equivalent to those obtained by Gueron and Levin (1995) with their own model.

#### Effect of population density and habitat openness

In the model of Bonabeau and Dagorn, groups entering the same site aggregate into a single group. So, a site can be considered as an area in which any individual perceives its conspecifics. If  $A$  designates the area available to the whole population, then the area of each site is  $\alpha = A/N$ . It follows that the mean size of groups at equilibrium is

$$\langle s \rangle = \sqrt{\frac{\alpha d}{2p}}$$

where  $d = n/A$  is the population density. It then appears that multiplying the area perceived by the individuals ( $\alpha$ ) or the population density ( $d$ ) by a factor  $k$  has exactly the same effect on the mean size of groups at equilibrium. The same is true with the model by Gueron and Levin (1995) and ours (Gerard and Loisel, 1995: appendix B).